



Delcourt, J., Bode, N., & Denoel, M. (2016). Collective Vortex Behaviors: Diversity, Proximate, and Ultimate Causes of Circular Animal Group Movements. *Quarterly Review of Biology*, 91(1), 1-24. <https://doi.org/10.1086/685301>

Peer reviewed version

Link to published version (if available):
[10.1086/685301](https://doi.org/10.1086/685301)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the accepted author manuscript (AAM). The final published version (version of record) is available online via University of Chicago Press at <http://dx.doi.org/10.1086/685301>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: <http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

COLLECTIVE VORTEX BEHAVIORS: DIVERSITY, PROXIMATE, AND ULTIMATE CAUSES OF CIRCULAR ANIMAL GROUP MOVEMENTS

JOHANN DELCOURT

*Laboratory of Fish & Amphibian Ethology, Behavioural Biology Unit, Department of Biology, Ecology and Evolution, University of Liège
4020 Liège, Belgium
e-mail: johann.delcourt@ulg.ac.be*

NIKOLAI W. F. BODE

*Department of Mathematical Sciences, University of Essex
Colchester, CO4 3SQ United Kingdom
Department of Engineering Mathematics, University of Bristol
Bristol, BS8 1UB United Kingdom
e-mail: nikolai.bode@bristol.ac.uk*

MATHIEU DENOËL

*Laboratory of Fish & Amphibian Ethology, Behavioural Biology Unit, Department of Biology, Ecology and Evolution, University of Liège
4020 Liège, Belgium
e-mail: mathieu.denoel@ulg.ac.be*

ABSTRACT

Ant mill, caterpillar circle, bat doughnut, amphibian vortex, duck swirl, and fish torus are different names for rotating circular animal formations, where individuals turn around a common center. These “collective vortex behaviors” occur at different group sizes from pairs to several million individuals and have been reported in a large number of organisms, from bacteria to vertebrates, including humans. However, to date, no comprehensive review and synthesis of the literature on vortex behaviors has been conducted. Here, we review the state of the art of the proximate and ultimate causes of vortex behaviors. The ubiquity of this behavioral phenomenon could suggest common causes or fundamental underlying principles across contexts. However, we find that a variety of proximate mechanisms give rise to vortex behaviors. We highlight the potential benefits of collective vortex behaviors to individuals involved in them. For example, in some species, vortices increase feeding efficiency and could give protection against predators. It has also been argued that vortices could improve collective decision-making and information transfer. We highlight gaps in our understanding of these ubiquitous behavioral phenomena and discuss future directions for research in vortex studies.

KEYWORDS

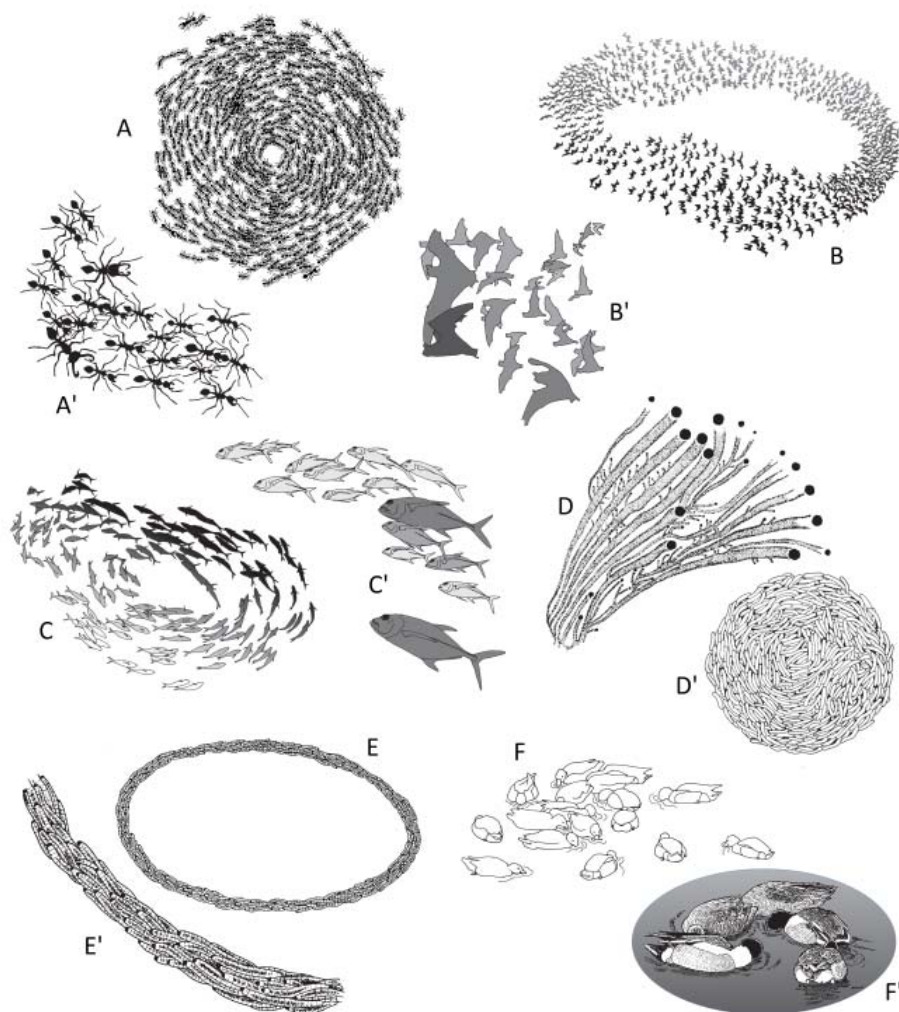
collective behavior, collective motion, group behavior, milling behavior, self-organization, torus

The present pdf is the author version. The publisher version of the paper is available in an institutional repository and in the publisher website: <http://dx.doi.org/10.1086/685301> (University of Chicago Press):

INTRODUCTION

Imagine it is dusk and you are watching a seemingly never-ending number of bats leave the cave in which they roost. Suddenly and for no apparent reason, a large number of them start to move in a circle around a clearly defined but unmarked center (Figure 1). For many seconds or even minutes, this moving “bat doughnut” persists in the sky. Now imagine you are in the ocean, watching schools of fish that move synchronously, almost behaving as one body. From one moment to the next—perhaps there was a predatory fish close by—the school forms a vortex of bodies very much like the bats (Figure 1). Again, it takes minutes before the milling movement of the group ceases. Why do fish and bats show such similar behavior? Why do they move around in a circle? How do they decide which direction to go without colliding?

FIGURE 1. VORTEX IN DIFFERENT SPECIES (IN EACH CASE A CLOSE-UP AND A WIDE VIEW OF THE COLLECTIVE BEHAVIOR). A) Mill in army ants (*Eciton* sp.). B) Flying doughnut in wrinkle-lipped bats (*Tadarida plicata*). C) Mill in jack fish (Carangidae, Teleostei). D) Vortex of *Bacillus* sp. bacteria: vortex are on the top of the branches in the large-scale view. E) Circle of armyworms (*Sciara militaris*, Fungus gnat, Sciaridae). F) Shoveler ducks vortex (*Anas clypeata*): close view represents some individuals in the vortex center. Drawings by A.-M. Massin and V. Briers.



The circular group movement described above is a typical example of collective behavior. Collective behaviors, the global dynamics or movement of groups resulting from the interactions of many individuals, are widespread in nature (e.g., Couzin and Krause 2003; Sumpter 2006, 2010; Couzin 2009). Investigations in the field and the laboratory, in computer simulations, and using robots have shown that a number of collective movement behaviors can arise from simple interaction rules between individuals (such as “avoid collisions”), as well as between individuals and their environment (e.g., “move toward food”; Couzin et al. 2002; Couzin and Krause 2003; Delcourt and Poncin 2012; Mitri et al. 2013; Tunstrøm et al. 2013). Three different major classes of collective motion can be observed in cohesive groups: “swarms”—when the movement synchronization within the group is weak and the group is almost stationary; “polarized schools”—when movement within the group is highly synchronized and the group shows directed movement; and “rotating circular formations” or “vortices”—when individuals turn around a common center. We focus on this last behavior, which has been described by a large number of similar or synonymous terms (see Table 1). Throughout, we adopt the term “vortex,” which is widely used in the scientific literature.

TABLE 1
Synonymous terms associated with collective vortex behaviors

rotating circular formation	swirling behaviors	doughnut
milling behaviors	moving circle	wheels
mills	whirling	ring
vortices	circular columns	boiling motion
rotating bangels	winding columns	convective movement
rotating spiral	whorl patterns	bioconvection
swirl	torus	circle pit

Vortex motions in animal groups have attracted the attention of scientists for over a century. In 1899, Jean-Henri Fabre reported the behavior of circular columns of pine processionary caterpillars (*Thaumetopoea pityocampa*) in his *Souvenirs Entomologiques*. He described how to arrange these caterpillars to achieve the formation of a continuous loop. Later, vortices were reported in army ants (*Eciton* sp.; Wheeler 1910; Schneirla 1944) and in juvenile schools of catfish (*Ameiurus* sp.; Parr 1927). Since these pioneering investigations, circular group movements have been found in many animal species, including insects, fish, amphibians, birds, and mammals, including humans. Even protists and bacteria vortices have been observed (Figure 1). Table 2 catalogs the reported cases of collective vortex behaviors in the literature.

To date, there is no definitive and generally applicable definition for vortex movements. It has been suggested that vortices are systems (e.g., groups of animals) in which there is a correlated radial motion of components of this system (i.e., individuals) around a common center (modified from Ben-Jacob et al. 1997). In an alternative classification, Gautrais et al. (2008) consider vortices as a particular case of swarms. This view is based on the similar global movement dynamics of swarms and vortices: the group speed is low (in comparison with individual speeds) and the degree of global alignment of individual movement directions is low. This contrasts with polarized schools where the global alignment of individual movement directions and global speed are high. Delcourt and Poncin (2012) take into account the local movement dynamics of groups. They suggest that vortices are a particular case of polarized schools that are characterized by a high degree of alignment of individuals’ movement directions to individuals nearby and, more generally, by a significant synchronization of movements.

TABLE 2
Diversity and function of collective vortex behaviors

	Taxa	Vortex type	Function	References
Eubacteria	Oxytactic bacteria: <i>Bacillus subtilis</i>	Bioconvection	Oxygenation; feeding	Cisneros et al. 2007
	Thermophilic bacteria: <i>Bacillus licheniformis</i> , <i>B. thermoglucosidasius</i>	Bioconvection	Temperature; choice; oxygenation; feeding	Choi et al. 2004; Kuznetsov 2005
	<i>Paenibacillus vortex</i> , <i>Bacillus subtilis</i> , <i>B. circulans</i> , <i>Archangium violaceum</i> , <i>Chondromyces apiculatus</i> , <i>Clostridium tetani</i>	Social vortex (short-range chemoattractant and long-range chemorepellent); reflective circular walls	Reduction of exposure to antibiotics; increasing mobility	Ben-Jacob et al. 1997; Ben-Jacob 2003; Czirik et al. 1996
Chlorophyceae	<i>Chlamydomonas</i> sp. <i>Dunaliella</i> sp. <i>Volvox</i> sp.	Bioconvection	Photosynthesis	Foster and Smydth 1980; Shitanda et al. 2007; Williams and Bees 2011
Euglenozoa	<i>Euglena</i> sp.	Bioconvection	Photosynthesis	Wager 1911
Stramenopiles raphidophytes	<i>Heterosigma akashiwo</i>	Bioconvection	Photosynthesis	Bearon and Grünbaum 2006
	<i>Phytophthora citricola</i>	Bioconvection	Dispersion?; finding host?	Ochiai et al. 2011
Alveolates	<i>Tetrahymena pyriformis</i> <i>Stenosernella nucula</i> <i>Paramecium tetraurelia</i>	Bioconvection	Oxygenation; feeding	Platt 1961; Kils 1993; Mogami et al. 2004; Kitsunezaki et al. 2007
Amoebozoa	<i>Dictyostelium discoideum</i>	Social vortex (cell-cell adhesion, chemical signal not necessary)	Locomotion?	Rappel et al. 1999

Hexapoda	Processionary caterpillars (Lepidoptera): <i>Thaumetopoea pityocampa</i>	Circular trails	No evident function	Fabre 1899
	Army ants (Hymenoptera): <i>Eciton</i> sp.	Circular trails	No evident function	Wheeler 1910; Schneirla 1944, 1971; Franks et al. 1991; Couzin and Franks 2003
	Armyworms (Diptera): <i>Sciara militaris</i>	Circular trails	No evident function	Delcourt and Poncin 2012
	Maggots (Diptera): <i>Lucilia sericata</i>	Bioconvection	Heat control; feeding	Charabidze et al. 2011
Crustacea	Water fleas (Cladocera): <i>Daphnia</i> sp.	Punctual attractive stimulus	Feeding	Ordemann et al. 2003; Vollmer et al. 2006; Mach and Schweitzer 2007
Chondrichthyans	Sharks: <i>Carcharhinus amblyrhynchos</i>	Social vortex? Punctual attractive stimulus?		Economakis and Lobel 1998
Teleostei	Very numerous marine and freshwater species (e.g., <i>Caranx</i> sp., <i>Sardinops</i> sp., <i>Notemigonus crysoleucas</i>)	Social vortex (largely the more frequent situation); constrained vortex		Parr 1927; Couzin et al. 2002; Parrish et al. 2002; Viscido et al. 2004; Gautrais et al. 2008; Delcourt and Poncin 2012; Tunstrøm et al. 2013
Amphibia	Anuran tadpoles: <i>Spea multiplicata</i>	Stigmergic vortex	Feeding	Bazazi et al. 2012
Aves	Gliding birds	Punctual attractive stimulus	Mobility	Alexander 2003; Pennycuick 2008; O'Neal Campbell 2015
	Ducks: <i>Anas clypeata</i> , <i>Anas rhynchotis</i> , <i>Malacorhynchus membranaceus</i>	Punctual attractive stimulus and stigmergic vortex	Feeding	Bode and Delcourt 2013
Mammalia	Bats: <i>Chaerephon plicatus</i>	Probable social vortex		Nill and Siemers 2001
	Bats	Constrained vortex or social vortex (close to or in cave)	Avoiding collision/synchronization of cave exit	Stuart 1994
	Humans	Social vortex (artificial rules chosen by experimenters or participants)		Dyer et al. 2009; Silverberg et al. 2013

The ubiquity of vortex behaviors may lead to the notion of common causes or fundamental underlying principles for this behavioral phenomenon across contexts. However, to date, no comprehensive review and synthesis of the literature on vortex behaviors has been conducted. Here, we review the state of the art of our understanding of vortex formation by highlighting that there is a multitude of proximate and potential ultimate mechanisms involved.

First, we introduce the general properties of vortex movements, such as their temporal and spatial scales, and the alignment of turning directions. Second, we review different proximate mechanisms that could explain vortex behaviors. At this point, we also discuss the transition between different collective behaviors, which facilitates understanding the conditions and reasons for vortex formation. Third, we discuss potential ultimate causes for vortex movements. Finally, we suggest new directions for research and draw conclusions that emerge from this review.

VORTEX PROPERTIES

Vortex Scales

The number of individuals involved in vortex behaviors is highly variable and depends on the organisms. The smallest vortex can consist of only two individuals, a case that can be observed in Northern shoveler ducks (*Anas clypeata*; Bode and Delcourt 2013). In contrast, bacteria vortices can include millions of cells circling in coordination around a common center (Ben-Jacob 2003). For most species, the number of individuals involved in vortex behaviors lies between these two extremes and vortices frequently consist of dozens or hundreds of animals. Some species only display vortex behaviors in sufficiently large groups. For instance, in spadefoot toad tadpoles (*Spea multiplicata*), a vortex is observed when the group size reaches several hundred individuals (Bazazi et al. 2012). Similarly, theoretical models and observations in fish shoals (i.e., groups of fish) show a dependence of group size in the adoption of vortex behaviors (i.e., Lukeman et al. 2009; Tunström et al. 2013; Calovi et al. 2014).

The smallest spatial extent of vortices is observed in microscopic species, such as bacteria (Ben-Jacob and Levine 2006) or protists (Rappel et al. 1999). However, it is perhaps more appropriate to consider the extent of vortices relative to the body size of the individuals involved. From this perspective, bacteria and ants display the most impressive known examples of vortex movement in the world. The explorer and naturalist William Beebe (1921) reported the observation of a legionary army ant mill (*Eciton burchellii*). This ant loop had a diameter of 365 meters, was six lines wide in many places, and it took the ants 2.5 hours to complete one revolution. Although this ant loop was probably not circular, Schneirla (1944) also reported smaller turning disk-shaped formations of ants (*Eciton praedator*).

The range of time scales over which vortex movements persist is also substantial. In this context we need to take into consideration that there are different mechanisms that lead to vortex movement, as we will discuss below, which can affect for how long vortex movements persist. Golden shiners (*Notemigonus crysoleucas*)—a cyprinid fish—adopt vortex movements for a few seconds or minutes, depending on the size of the shoal (Tunström et al. 2013). In contrast, some vortices have a long life span and last as long as no perturbation stops them. Amoeba such as *Dictyostelium discoideum* can rotate for tens of hours in the same direction (Rappel et al. 1999) and Fabre (1899) reported caterpillar circles turning for seven days. Perhaps the most extreme example is that of an ant mill that lasted for seven days and only ended because of the starvation or dehydration of the ants (Schneirla 1944). However, we must keep in mind that in some species, vortex movements can be more fluid in that individuals can continuously join or leave the vortex. In this case, a long vortex life span does not necessarily imply that the same individuals are involved throughout the whole duration of this group behavior.

Direction of Rotation in a Vortex

Both clockwise and anticlockwise movement directions can be observed in all known examples of vortex collective behaviors. In a typical vortex, the majority of individuals move in the same direction. When several vortex movements occur simultaneously, both movement directions can be adopted, but each separate vortex adopts only one direction (e.g., in bacteria: Czirák et al. 1996; Ben-Jacob et al. 1997; Ben-Jacob 2003). We further discuss the mechanisms for movement direction choices in the section, Choice of Vortex Directionality.

MECHANISMS (PROXIMATE CAUSES)

Nonsocial Attractive Force

The simplest way to generate a vortex is via individual attraction to a localized stimulus concentrated in a small area, under the conditions that, first, a nonzero individual speed is maintained and, second, individuals cannot occupy the same location and must avoid collisions (Figure 2A). This mechanism presents a way in which large numbers of individuals can aggregate at high densities without social attractive forces acting between individuals. A vortex centered on this stimulus can form under such conditions and persists until the attractive potential of the stimulus disappears. We discuss the mechanism for how collision avoidance alone can result in all individuals moving in the same direction around a vortex center in the section, Choice of Vortex Directionality.

The case of water fleas (*Daphnia* sp.) turning around a light beam perfectly illustrates this situation. These cladoceran crustaceans are strongly attracted to light, since exposing water to sunlight stimulates the production of phytoplankton, *Daphnia*'s prey. When *Daphnia* are placed in a dark aquarium with a vertical flashlight beam, they rapidly move first toward the light beam and then start rotating around it (Vollmer et al. 2006). Initially, rotation in both directions can be observed but, after some time, the *Daphnia* spontaneously align their movement directions. Individual-based computer simulations based on the behaviors described above (attraction to stimulus and collision avoidance) reproduce this vortex behavior and its onset (Vollmer et al. 2006; Mach and Schweitzer 2007).

Nonsocial Repulsive Force

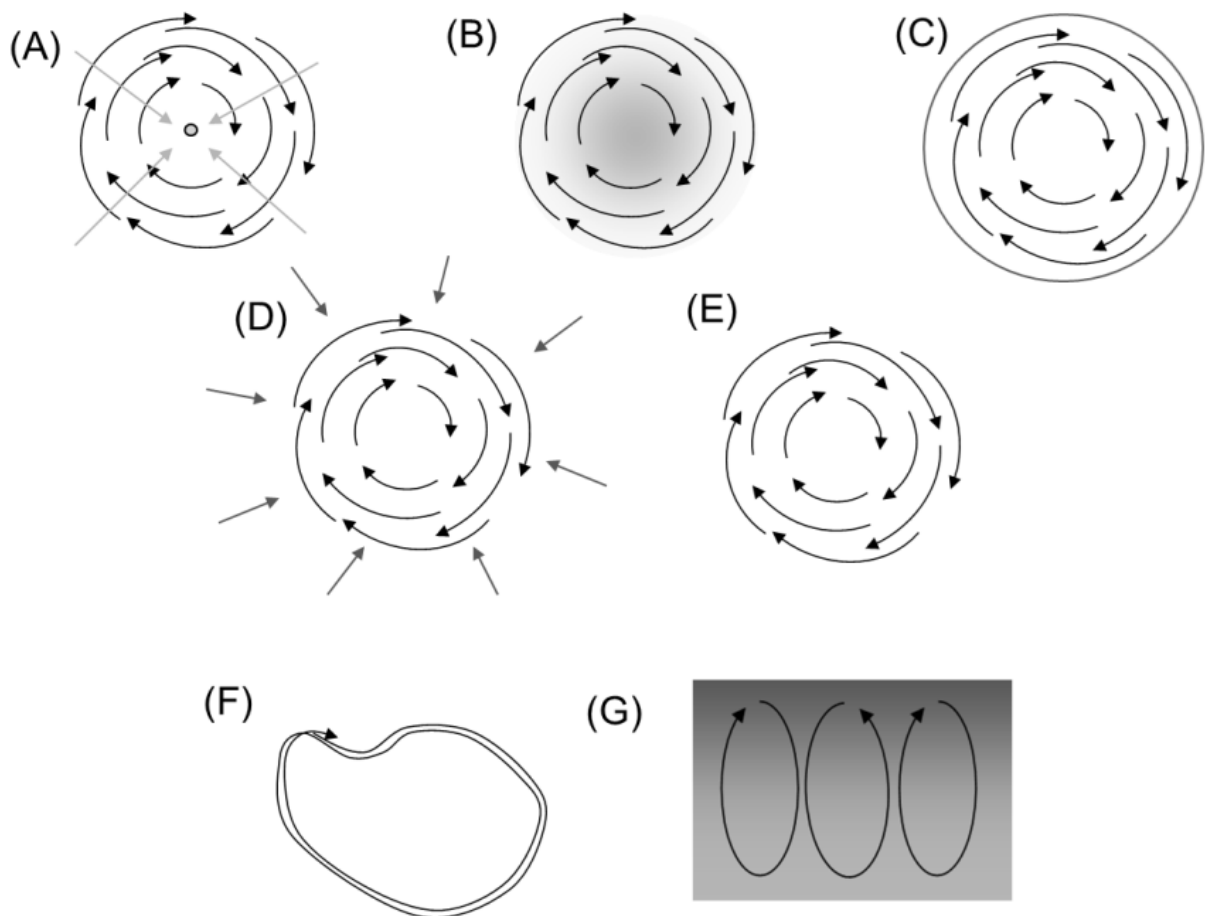
The opposite of attraction, repulsion, can have a similar effect. Environmental constraints surrounding animal groups (e.g., obstacles or walls; Figure 2C) or repelling stimuli on the periphery of groups (e.g., predators; Figure 2D) can concentrate individuals in small areas. If individuals continue to move, collective vortex behaviors can result in a similar way to what we have discussed above (collision avoidance or additional social interactions leading to alignment). For example, fish in tanks can be restrained by tank walls and bats in caves by the cave walls. Computer simulations show that this is a potential mechanism to create vortex movements only through the effect of such boundaries and a repulsive social force to avoid collision between individuals. To give an example, some of these models implement reflective circular walls and a short range “hard-core” repulsion to avoid aggregation of individuals in small areas (Czirák et al. 1996; Czirák and Viscek 2000; Grossman et al. 2008). These vortex movements are maintained for as long as the environmental constraining forces persist or until individuals intentionally interrupt this behavior.

Stigmergy

Stigmergy can be defined as the modification of the environment by the behavior (e.g., movement) of an individual that subsequently affects the behavior of other individuals (Grassé 1959). It is thus a mechanism of self-organization without direct communication or interaction between individuals that can

lead to collective behaviors (Beckers et al. 1994; Theraulaz and Bonabeau 1999; Camazine et al. 2001). Stigmergy can lead to vortex movements in two ways. First, the movement of individuals can create locally favorable conditions that attract more individuals via positive feedback. If individuals have to keep moving, this can lead to a vortex in a similar way to the nonsocial attractive forces discussed in the section, Nonsocial Attractive Force (see also the section, Choice of Vortex Directionality; Figure 2B). The difference is that the attractive potential is created by individuals and not by other external factors such as light, for example. Second, well-known examples for stigmergic interactions are the chemical trails laid by individuals and followed by individuals of the same species (e.g., pheromone trails in ants). When these trails form a loop, they can induce circular movement in animal groups. We will discuss this mechanism in greater detail in the next section, A Special Case of Stigmergy: Trail Reinforcement.

FIGURE 2. SCHEMATIC ILLUSTRATION OF DIFFERENT MECHANISMS UNDERLYING COLLECTIVE VORTEX BEHAVIORS. Black arrows indicate the trajectory of some individuals. A) Attraction to a single stimulus, individuals are not (necessarily) attracted by other group partners. Gray arrows represent the attractive force toward the stimulus, which is indicated by the central dot. B) Stigmergy: the activity of individuals creates an attractive area. This area is indicated by gray gradient. C) A surrounding constraint (gray circle) confines individuals and limits their movements. D) Surrounding repulsive stimuli. Gray arrows represent the repulsive force to these stimuli. E) Collective vortex behavior arising from social interactions between individuals (social vortex). F) Circular trail in which individuals follow the trail laid by other individuals. G) Bioconvection under an initial gradient (illustrated by the gray gradient).



Mexican spadefoot toad tadpoles (*Spea multiplicata*) forage in groups and adopt a slowly rotating circular formation (Bazazi et al. 2012). This behavior has been hypothesized to act as a means to agitate the substratum of shallow ponds and thus to improve food intake. Bazazi et al. induced this vortex behavior experimentally by providing a central food patch, which resulted in circular movement of individuals that grew over time in mobilizing increasing numbers of individuals. Based on their experiment, the researchers suggest a positive feedback mechanism for the growth of an initial vortex nucleus. Higher densities of tadpoles (resulting from tadpoles aggregating around food) result in faster water flow due to individuals displacing water by beating their tails. This increased flow orients and aligns tadpoles, as individuals turn to face into the water flow (rheotaxis), which subsequently increases the flow through positive feedback. In addition, the water current suspends and transports nutrients, which reinforces the swimming direction of the tadpoles. This vortex movement is a case of stigmergy because the movement of individuals alters the local environment (water current and nutrient availability), which in turn affects the behavior of other individuals.

Filter-feeding ducks adopt swirling behaviors alone, in small groups, or in larger vortices of several tens of individuals (Bode and Delcourt 2013). It has been hypothesized that this swirling movement causes nutrients to rise to the surface, allowing the birds to filter it from the water (Johnsgard 1965; Todd 1979; Gooders and Boyer 1986). Bode and Delcourt (2013) suggest a mechanism for the onset and maintenance of such vortex group movements based on a simulation model. The model assumes that the only social interaction between individuals is collision avoidance. Otherwise, individuals have a tendency to swim toward higher nutrient concentrations. The crucial ingredient of the model is the way in which individuals interact with the resource landscape containing nutrients. Individuals can consume nutrients, but can also release additional nutrients from the substratum through their movement. If the quantity of nutrients released by movement is high enough, local attractive potentials can form. Adjusting the relative strength of nutrient consumption and release results in different collective behaviors, including vortex movements as described above. Importantly, these different collective behaviors arise in an initially homogeneous nutrient distribution. It is the indirect stigmergic interactions between individuals that result in collective behaviors.

It has been suggested that vortex movements of bacterial colonies are based on stigmergic interactions. Several bacteria species (e.g., *Bacillus subtilis*, *B. circulans*, *Paenibacillus vortex*) are able to develop a “vortex morphotype” where colonies grow arms or branches outward from a nucleus in a circular motion (Figure 1D). Smaller vortices can also emerge inside the colony, sometimes giving rise to a new arm or branch. Czirók et al. (1996; see also Ben-Jacob et al. 1997; Ben-Jacob 2003) present a detailed individual-based model for the formation of such bacterial colonies, suggesting that bacteria emit and react to chemoattractants and chemorepellents. These indirect interactions lead to vortex movements in a similar way to what we have described above. As an additional mechanism, Czirók et al. (1996) introduced long-range, chemically mediated, repulsive interactions: when individuals fail to obtain sufficient quantities of nutrients, they become immobile and emit a chemical that repulses other bacteria. This mechanism causes bacterial vortices to avoid other colonies and areas that have previously been depleted of nutrients. Simulations demonstrated that this model can reproduce a variety of observed bacterial colony shapes, including disk-shaped vortices and irregular rings of moving bacteria (Czirók et al. 1996).

A Special Case of Stigmergy: Trail Reinforcement

Pheromones have the clear function of facilitating communication between individuals of the same species or even colony. They provide localized information that persists over significant periods of time (Deneubourg et al. 1990; Dorigo et al. 2000; Perna et al. 2012). Such a communication via pheromones in insect trail formation is often considered as a case of stigmergy (Theraulaz and Bonabeau 1999; Dorigo et

al. 2000; Garnier et al. 2007). Individuals release pheromones and thereby create a trail that others follow. However, the only modification of the environment to initiate the trail behavior is the accumulation of pheromones. Sometimes a contingent event (for example, having to turn back in the face of an obstacle or walking around the perimeter of an obstacle) can cause the trail to rejoin itself, thereby creating a loop. In some insect species, these closed pheromone trail loops result in the circular movement of many individuals. These circular columns can be just one individual wide, as in processionary caterpillars (Fitzgerald 2003; Figure 2F), or they can change from a ring into a turning disk, such as in ants (Schneirla 1944, 1971; Figure 1A).

Although the question of the initial event leading to the formation of these phenomena is interesting, it is more pertinent to understand why and how the circular motion is maintained, often for very long periods. The insect mills are the result of a positive feedback mechanism: the production of a signal that is enhanced by accumulation in the same location, thereby maintaining the circular path (Deneubourg et al. 1989; Franks et al. 1991; Fitzgerald 2003). For example, in ants, the initial accumulation of pheromones results in an increase of the mean speed until it reaches a threshold when the pheromone concentration does not increase any further (Deneubourg et al. 1989; Franks et al. 1991). Interestingly, there does not appear to be a mechanism to stop this positive feedback and consequently the circular motion can be maintained for long periods of time.

Social Forces

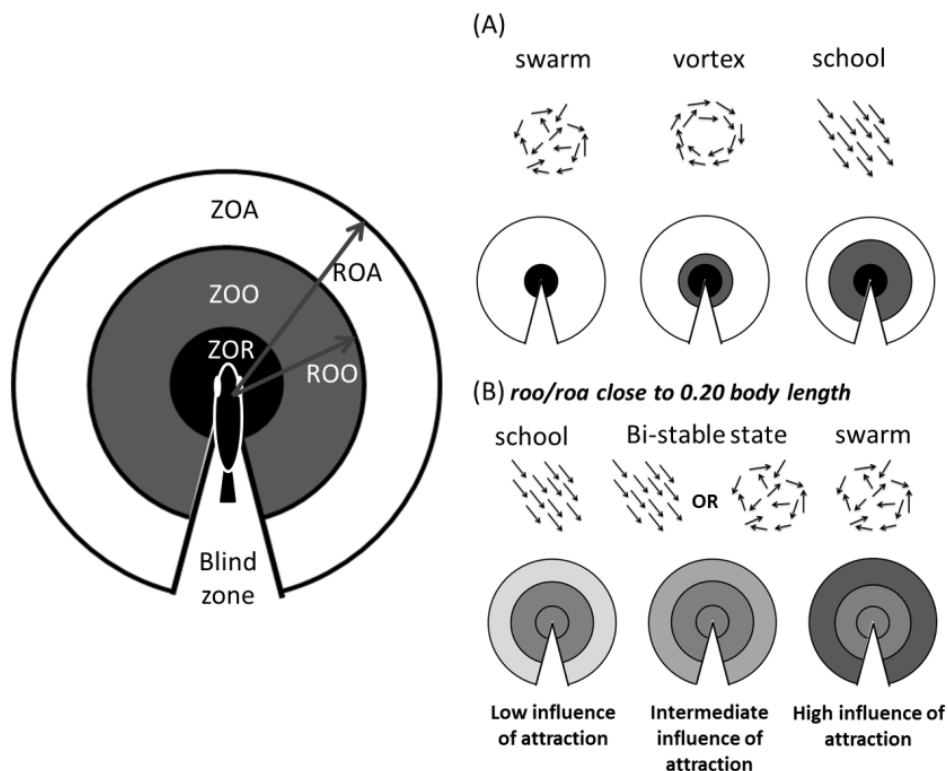
In the absence of nonsocial attractive or repulsive forces (e.g., environmental, stigmergic, predatory), another mechanism for the formation of collective vortex behaviors is via direct interactions between individuals that are typically mediated by short-lived visual or sound stimuli.

Individual-based models allow exploring the effect of different social interactions on the movement dynamics of animal groups (e.g., Aoki 1982; Reynolds 1987; Huth and Wissel 1992; Couzin et al. 2002; Parrish et al. 2002; Bode et al. 2010, 2011). In these models, individuals typically follow three behavioral rules (Figure 3): first, move toward other individuals; second, avoid collisions with other individuals; and, third, align with the movement direction of other individuals. Models are often based on the assumption that the behavioral rule describing the interaction between two individuals depends on the distance between them. For example, nearby individuals adjust their movement to avoid collisions and individuals farther apart move toward each other to maintain group coherence. Simulations have shown that this basic concept can explain different states of collective movement, including vortices, in a large range of taxa such as cephalopods, crustaceans, birds, and mammals (namely ungulates and humans; Couzin and Krause 2003; Sumpter 2010; Silverberg et al. 2013). For example, Couzin et al. (2002) showed that modifying the relative range of the distinct behavioral rules can result in different types of collective movements, such as polarized schools, swarms, and vortices (Figure 3A). Vortices emerge from the simulated interactions between individuals when collision avoidance and movement alignment interactions are restricted to individuals who are close to each other whereas attraction acts between individuals further apart. A long range of attraction ensures that all individuals essentially get attracted to the center of the group. A relatively short range of orientation means that they cannot all align. If the range of alignment interactions is increased, the vortex movement breaks down and the group moves as a polarized school. Similar results can be achieved if, instead of varying the spatial range of interaction behaviors, individuals follow the different rules according to different relative weightings (Gautrais et al. 2008; Figure 3B).

It has been suggested that animals adjust the spatial range or relative weighting of the different behavioral rules according to their internal state. For instance, attraction could be prioritized in antipredation behavior, resulting in vortex movements (Beecham and Farnsworth 1999; James et al. 2004). Interestingly, simulations have shown that when all of the individuals in a group simultaneously change their behavioral parameters (e.g., decrease the range or strength of alignment interactions), this

does not necessarily imply that the group adopts the movement patterns usually associated with the new set of behavioral parameters (Couzin et al. 2002; Gautrais et al. 2008). This is because of a hysteresis effect, the property of some dynamical systems to maintain a dynamical state even when the required parameter values for the formation of this state are no longer given. Such hysteresis effects need to be considered when investigating the presence or absence of vortex movement states in socially interacting animal groups.

FIGURE 3. ILLUSTRATION OF INTERACTION RULES IMPLEMENTED IN METRIC MODELS FOR COLLECTIVE MOTION. The way two individuals interact is dictated by the distance between them: an individual moves away from others within its zone of repulsion (ZOR), aligns its movement direction with individuals in its zone of orientation (ZOO), and moves toward individuals within its zone of attraction (ZOA). Individuals cannot perceive others located within their blind zone (by vision or other perception organs). Radius of orientation (ROO) and radius of attraction (ROA) are the outer radii of ZOO and ZOA. (A) Couzin et al. (2002) showed that changing the relative extent of the interaction zones generates different collective behaviors. A large ZOA and absence or quasi-absence of ZOO induces swarming behavior, a moderate ZOO induces vortex behaviors, and a large ZOO induces a polarized group. (B) Gautrais et al. (2008) in some of their simulations, based on Couzin's model, did not modify the size of the interaction zones but varied the weighting of attraction (high weightings are illustrated by darker shades of gray). At ROO/ROA ratios close to 0.2, at intermediate influence of attraction such as in Couzin's model, the computer simulations produce a bistable state, where an aligned schools or a vortex are observed, depending on initial conditions. Gautrais et al. (2008) do not distinguish swarm and vortex movements in their simulations. However, when the influence of attraction is high, vortex movements are systematically observed; and when this influence is low, polarized schools are systematically adopted.



Even without changes in individual behavior, transitions between the different collective movement states (vortex, swarm, and polarized school) have been reported in laboratory environments. Tunstrøm et al. (2013) conducted pioneering work on the adoption of different collective movement states in the absence of external stimuli by analyzing long video recordings of the movement of undisturbed golden shiner schools. The authors observed frequent transitions between swarm, polarized school, and vortex states. For a fixed experimental tank size, the size of groups had an effect on the stability of the different movement states and the frequency of transitions, but not on the relative frequencies of transitions between movement states. The authors also suggest that transitions between movement states are influenced by interactions of individuals with both the tank boundaries and the movement of other group members.

Extensive simulations of an individual-based model by Calovi et al. (2014) also show that for particular parameter values of the model, both polarized schools and vortex movements can be observed, with frequent transitions between the two collective behaviors. Calovi et al. (2014) additionally show that vortex movements are only adopted after a threshold value of the group size is reached. Calovi et al. (2014) did not explore how group size affected the frequency of transitions between polarized schools and vortices.

These findings lead to an important observation: changes in collective movement states can occur as a result of changes in individual behavioral rules, but they can also occur for unchanged individual behavioral rules. This illustrates the difficulty in determining the precise mechanisms involved in the adoption of vortex movement states in socially interacting animal groups. Furthermore, this observation is of crucial importance for our discussion on ultimate causes for vortex movements (see the section, Ultimate Causes).

Bioconvection

Another mechanism for the formation of vortices is by bioconvection—when an aggregation of individuals forms a convective cell in which “currents” of individuals move in opposite directions. This phenomenon is well known in fluid dynamics and occurs when density differences inside a body of gas or liquid induce currents in opposite directions (Batchelor 2000; e.g., the movement of air during the formation of clouds). Similar processes can occur in aggregations of individuals when the density of individuals is very high (Hill and Pedley 2005). In bioconvection, individuals climb a gradient (e.g., toward warmth or higher oxygen concentrations), which results in the concentration of individuals in one location. At some point, the high concentration of individuals becomes unstable and individuals get pushed out of the favorable location by the arrival of additional individuals. Under spatial constraints, this mechanism can lead to the creation of a convective cell with currents in opposing directions (Platt 1961).

Bioconvection has been found in a large variety of species, particularly in microorganisms, such as ciliated and flagellate algae, bacteria, oomyceta, ciliophora, and insect maggots (Table 2). One example for this phenomenon is given by oxytactic (aerobic) bacteria in liquids. The oxygen-rich zone close to the liquid’s surface induces cells to accumulate at this upper boundary and results in high bacteria densities close to the surface (Dombrowski et al. 2004; Kuznetsov 2005). When the density of cells reaches a threshold, the bacterial layer becomes unstable, and since the cells are heavier than the liquid, they sink under the influence of gravity. Thus, the bacterial layer breaks into a collection of convective cells with rising and falling currents. The mechanism for the creation of these convective cells is based on two types of bacterial taxis: bacteria climb the oxygen gradient and are pulled downward by gravity. A third supplementary taxis, gyrotaxis, results from the convective motion itself. Gyrotaxis describes the cell movement resulting from the torque acting on the bottom-heavy cell due to gravity and the torque acting on the cell due to viscous forces arising from local shear flows (Ghorai and Hill 1999). This causes cells to move toward regions of locally downwelling fluid and away from upwelling fluid (Kessler 1985a,b).

Choice of Vortex Directionality

Whether all of the individuals inside a vortex move in the same direction or not and how long it takes individuals to align their movement directions inside a vortex can be indicative of underlying mechanisms. For example, fast and synchronous aligning of movement direction suggests the presence of social interactions described in the section, Social Forces. In the absence of such social interactions, the bi- or unidirectionality in a vortex depends on the density of individuals. As a vortex is formed, the probability of colliding or having to avoid collision with another individual is directly dependent on the local density of individuals. Both collision and collision avoidance result in modifications of individual movement directions. When the number of individuals moving in one direction, say clockwise, outweighs the number of individuals moving in the anticlockwise direction, the latter have (on average) a higher probability of changing their movement direction toward the clockwise direction. Thus, over time, all individuals align their movement direction to clockwise. When this happens, collisions and collision avoidance movements are infrequent and the system becomes stable. Low densities of individuals may result in insufficiently frequent collision and collision avoidance interactions to lead to alignment under this scenario. This mechanism is largely supported by vortex movements observed in water fleas *Daphnia* sp. (Ordemann et al. 2003; Vollmer et al. 2006; Mach and Schweitzer 2007; see also experiments of collective choice of direction in locusts and prawns placed in annulus, respectively Buhl et al. 2006 and Mann et al. 2012) and can easily be simulated. In ants, observations and computer simulations (with similar avoidance behaviors) show a tendency to run in the same direction as the majority in the initial conditions (Franks et al. 1991; Couzin and Franks 2003). If by chance equal numbers of ants were running in both directions, it can take a very long time for one direction to dominate (Franks et al. 1991).

Another potentially stable structure with regard to collision and collision avoidance is the existence of multiple concentric circular lanes moving in opposite directions. Linear lane formation (spontaneous adoption of parallel bands) is known to increase the flow of ants to and from the nest (Couzin and Franks 2003) and frequently occurs in human pedestrian crowds moving in corridors, walkways, or on crossroads (Milgram and Toch 1969; Helbing and Molnár 1995; Couzin 1999; Moussaïd et al. 2009, 2011). In the context of vortex movements, bidirectionality has to date not been observed in lane-forming ants (Couzin and Franks 2003); moreover, bidirectional lane formation is not reported in any other species performing circular group movements. The experiment reported by Dyer et al. (2009), where the movement of 200 human participants in a circular area led to a vortex with multiple lanes moving in opposite directions, is the only example of this scenario known to date. However, this experiment does not represent everyday human behavior.

Global changes in movement direction have been studied systematically in juvenile desert locusts moving in an annular arena, where the probability of global changes in movement direction decreases with the density of individuals (Buhl et al. 2006). This coordinated motion in locusts is strongly influenced by cannibalistic interactions. Individuals in marching bands tend to bite others but risk being bitten themselves. Individuals can reduce their risk of an attack by aligning with neighbors (Bazazi et al. 2008, 2010). This effect is accentuated in high densities of individuals, so the changes of direction become rarer.

ULTIMATE CAUSES OF VORTEX FORMATIONS

The coordination of individuals in a vortex pattern could potentially result in advantageous collective properties allowing each individual to obtain energy, survival, or other fitness benefits that it would not receive when adopting a solitary behavior or social behaviors different from vortex behaviors (e.g., schooling or swarming). In this section, we discuss possible evolutionary origins for collective vortex movements and mention cases of this phenomenon that appear to be maladaptive or even accidental.

The key question regarding the ultimate causes of vortex movements is whether the behaviors underlying these movement phenomena can be selected for independently. As already mentioned in our review of proximate mechanisms above, there is evidence suggesting that, in some contexts, this may not be the case. For example, the vortex movements of trail-forming insects (see the section, A Special Case of Stigmergy: Trail Reinforcement) appear to be accidental and in the section, Maladaptive Examples, we argue that selection against behaviors that can accidentally lead to vortices would on average reduce fitness in these species. Furthermore, Tunström et al. (2013) and Calovi et al. (2014) have shown that social animals can and do display vortex movements, as well as other movement states for the same underlying individual-level social behavioral rules (see the section, Social Forces). In this case, independent selection for vortex movements is impossible and a broader perspective, which also takes alternative movement states into consideration, has to be adopted. More work is needed to develop a comprehensive explanation of the ultimate causes for vortex movements in such situations and hereafter we therefore restrict ourselves to reviewing examples of maladaptive vortex movements and possible advantages individuals could derive from vortex movements.

Maladaptive Examples

It has been observed that only after seven days of circular motion do caterpillars finally start altering their behavior, by not always strictly following the individual in front (probably as a consequence of starvation and dehydration) and therefore manage to break the vortex movement (Fabre 1899). Without external perturbation, army ants (*Eciton* sp.) can move in a vortex until they die of exhaustion or dehydration (Schneirla 1944, 1971; Franks et al. 1991; Gotwald 1995). Even if individuals do not die of starvation or dehydration in these examples, they suffer from a significant loss of energy and time when participating in the vortex movement. This loss of time and energy can have indirect (less time for reproduction or feeding) or direct (predation) fitness consequences for individuals. In these particular cases, the collective vortices appear to be a trap that individuals cannot leave without an external perturbation or internal disorder. It is not clear if these examples for maladaptive vortices occurred as a rare and accidental side effect when social behaviors evolved or if they occurred when animals were exposed to novel conditions they had not evolved to cope with (see the concept of “evolutionary trap” in Robertson et al. 2013). Although the accidental adoption of vortex movements of insects appears to be maladaptive, we have to keep in mind that, in general, insect trails are a powerful social behavioral adaptation to explore and exploit the environment. Overall, the significant advantages for individuals in terms of survival and (direct and/or inclusive) fitness derived from trail formation behavior outweigh the disadvantages and these vortices are therefore just a collateral epiphenomenon of adaptive social behavior.

Feeding Function and Access to Other Resources

In some cases, vortex movements could lead to benefits for all individuals involved. Each individual may act selfishly, but the global dynamics that result from individual actions lead to favorable conditions that result in fitness benefits for each individual. For example, in aquatic environments, filter-feeding species could derive an advantage from adopting vortices by releasing and suspending additional nutrients in the water. One example of this benefit of vortices is given by Mexican spadefoot toads (Bazazi et al. 2012). The importance of vortices for nutrient acquisition is supported by the result that food-deprived tadpole groups adopt collective vortex movements more frequently (Bazazi et al. 2012). A second example for collective feeding benefits of vortices could be given by shoveler ducks, where their circular motion causes nutrients to rise to the surface and thus allowing the birds to filter it from the water (Bode and Delcourt 2013).

Bioconvective cells occur in environments within initially heterogeneous resource distributions (see the section, Bioconvection). Over time, these vortex movements ensure that all involved individuals can periodically have access to the best locations, such as that one with the best temperature (e.g., improving

metabolism in maggots; Charabidze et al. 2011), the best access to light (e.g., in photosynthetic microorganisms; Williams and Bees 2011), or the best access to oxygen (e.g., in bacteria; Ben-Jacob 2003). Moreover, the collective motion can change the resource distribution (e.g., by creating currents in fluids), which may help reduce differences in oxygen and nutrient concentrations (Cisneros et al. 2007) or temperature (Choi et al. 2004; Kutznetsov 2005) across locations.

Obligate swimmers are species of fish that need to swim in order to breathe. For these species, adopting vortex movements may be beneficial because individuals could combine continued motion with energetic savings as a result of swimming in the slipstreams of others (Couzin et al. 2002, Hemelrijk et al. 2015; Marras et al. 2015). However, only a very small number of obligate swimmer species are known, such as some sharks (Carlson et al. 2004; Dowd et al. 2006), paddlefish, and tuna (Burggren and Bemis 1992; Wegner et al. 2010). This need to breathe can therefore not explain the adoption of collective vortex movements in many fish species.

Locomotory Function

By our definition, vortices are moving groups that turn around a well-defined center and have little to no net group speed. At first sight, this makes it unlikely that vortex movements could be beneficial for an individual's locomotion. However, for bacteria, vortex movements represent a mechanism that facilitates individual locomotion. Some bacteria move on hard surfaces by cooperatively producing a wetting fluid in which they swim. When placed on hard, nutrient poor surfaces, these bacteria have to solve the problem of accessing sparse nutrients while moving on an unfavorable surface. The bacteria solve this problem by generating a branching colonial organization (Ben-Jacob 2003). In this context, vortex movements provide the high bacterial densities necessary for movement. Once formed, vortices expand and translocate as a unit. In this way, bacteria colonies translocate in space when direct motion over the hard surface is impossible.

Antipredator Function

It has been suggested that one advantage of living in a group is a reduction in the time required to detect predators ("many eyes principle"; Lima 1995; Rieucau and Martin 2008). Adopting a vortex configuration allows groups to detect predators in all directions, which could be particularly useful for organisms with a large blind spot in their visual field. However, computer simulations show that increasing the blind spot or angle (see Figure 3 for a definition of this angle) decreases the adoption of vortex and other collective behaviors because it increases the probability that a group will split up (Gautrais et al. 2008).

Tunstrøm et al. (2013) note that in the event of a predatory attack, the local alignment inside a stationary vortex (in contrast to a "swarm" movement) could be advantageous, as the fast propagation of evasive individual behaviors in a synchronized way by the perception of behavioral change of close neighbors would be optimal. In contrast, Gautrais et al. (2012) suggest that the absence of local alignment in swarm movements could be a favorable condition for a "flash expansion" maneuver (a frequent collective antipredator behavior). To date, it has not been shown conclusively that adopting vortex behaviors helps to reduce the risk of predatory attacks to individuals in comparison to other collective movement states.

Wood and Ackland (2007) investigated the evolutionary stability of collective behaviors to predation using an individual-based model for the movement of socially interacting animals. Their simulations implement selection via predation through the presence of small random mutations to the way in which individuals balance the behavioral rules described in the section, Social Forces, the size of the blind spot in an individual's visual field, and their speed. The simulations suggest that two collective behaviors can

be selected: fast-moving dynamic polarized groups or slow-moving groups that can adopt vortex formations. The latter behavior is enhanced in prey when predators have a large viewing angle. In these simulations, it is difficult to disentangle the specific benefit of adopting vortices compared to other movement states in the slow-moving groups. However, according to these simulations, the success of predators is not affected by the presence of vortex behaviors in slow-moving groups, while it decreases significantly in dynamic polarized groups. This suggests that although slow-moving groups that can display vortices are not the globally optimal option for survival, they constitute one outcome of the evolutionary process. The vortex behaviors that evolved in these simulations can be interpreted as the local expression of the “selfish herd” hypothesis (Hamilton 1971; Morton et al. 1994), in that individuals dynamically reduce their risk of being predated by hiding within the group (Wood and Ackland 2007).

Kunz et al. (2006) proposed another evolutionary model for prey movement under predation. In contrast to Wood and Ackland (2007), this model assumes that prey cannot perform any evasive movements away from the predator. Behavioral strategies for individuals were encoded in simple neural networks. The sensory field of each prey is separated into sectors that encode interaction zones (repulsion, attraction, and alignment, as in Figure 3) and capture the directionality of individual’s responses to others. Information from these different sectors is weighted and mapped to a behavioral output via the neural networks. The weights for the input from each sector in the neural network are selected for during evolutionary runs as a function of the survival rate of individuals. Based on these simulations, Kunz et al. found that under predation, prey evolved different behavioral strategies. The most frequent strategy adopted led to highly polarized schools of prey. The behavioral strategy selected with the second highest frequency led to vortex formations in the prey. An interesting conclusion suggested by this model is that prey survival rates are much higher for polarized schools or vortex movements than for any other dynamic state groups can adopt, such as swarms (Kunz et al. 2006).

Collective Decision-Making and Information Transmission

Another potential benefit that an individual can derive from adopting collective vortex movements is the facilitation of information transfer and collective decision-making processes. Tunstrøm et al. (2013) suggest that fish vortices allow individuals to be locally polarized, which could be important for information transfer, while allowing the group to remain in a specific area. It has been suggested that in fish, the individual at the front of a school plays a major role in determining the directional decisions of the group (Bumann and Krause 1993; Miller et al. 2013). To our knowledge, there is no evidence that specific positions in vortices give one or several individuals an increased influence on the collective decision when choosing a movement direction. A vortex could represent an undecided group (in the sense that no consensus on the movement direction exists). In this movement state, every fish can have a more or less similar weight in the decision-making process and every fish can take the initiative to induce a group motion in a particular direction leaving the vortex (see Tunstrøm et al. 2013 for examples of such transitions). If a sufficient number of individuals follow the initiating fish, it becomes a temporary group leader. Alternatively, the movement initiation to break the vortex can be aborted and thus the vortex behavior is maintained until a consensus on a new movement direction is reached. Individuals in possession of additional information (e.g., location of food, presence of predator) could use this behavior of movement initiation to induce the group to follow them. However, it is difficult to say if this decision-making is a real social cognitive choice or essentially directed by external factors. Tunstrøm et al. (2013) suggest that, in their experiments, the transition from vortex to school seems largely mediated by internal stochastic effects and environmental factors (e.g., boundary effect).

FUTURE DIRECTIONS

Even though vortices are widely observed in biological systems, ranging across several orders of magnitude in both temporal and spatial scales, quantitative analyses are rare. However, improved technologies, such as computers capable of simulating collective behaviors in large groups (Bode et al. 2011; Tunstrøm et al. 2013), advances in motion tracking from videos (reviewed in Delcourt et al. 2013; see also Delcourt et al. 2011), and robots that can be integrated in animal groups (Halloy et al. 2007; Mitri et al. 2013) now facilitate the quantitative investigation of this phenomenon. Based on the few studies already taking this approach (Bazazi et al. 2012; Tunstrøm et al. 2013), this should greatly contribute to our understanding of collective vortex movements.

At present, the properties of collective vortex movements in biological systems have not been explored in detail. For example, the variation of individuals' speed, body orientation, density, and degree of alignment across vortex structures is currently largely unknown. In addition, the effect of the number and the density of individuals on these properties are largely unknown, except in the cases we mention above. The dynamics of vortex formation have not yet been studied in detail, and the fact that some vortices have an empty core and others do not is not well understood. Since only a small number of scientists have investigated some of these aspects of collective vortex movements by using different methodologies and summary statistics, a more detailed comparison of this phenomenon between different species is difficult.

In models for collective behavior, it is often assumed that groups consist of identical individuals that follow the same behavioral rules (e.g., Sumpter 2010). However, there is considerable evidence suggesting that individuals vary in their behavioral profile, even within groups (Sih et al. 2004; Michelena et al. 2010; Carter et al. 2013). How this heterogeneity of groups affects the global and internal dynamics of groups is to date not fully understood. On one hand, it is possible that individuals within groups do not have the opportunity to express or deliberately suppress their individual characteristics, adopting behaviors similar to other group members (Herbert-Read et al. 2013). In this case, group membership acts to reduce the expression of behavioral heterogeneity among individuals. On the other hand, it is possible that heterogeneity in individual behaviors impacts directly on group movement dynamics. For example, it has been shown that hungrier individuals (in schools of fish; Krause et al. 2000) or faster individuals (in computer simulations; Couzin et al. 2002) have a tendency to be located at the front of moving groups. Computer simulations have also shown that individuals with a stronger tendency to move toward others (higher attractive social force) take up positions closer to the center of the group, while individuals with weaker tendencies to move toward others occupy the group's periphery (Belmonte et al. 2008). Different positions within groups could provide significant fitness benefits for individuals (Krause et al. 1992, 1998). For example, predatory attacks may be most likely to occur at the front of schools (Bumann et al. 1997; Krause et al. 2000). More generally, heterogeneities within groups can induce self-sorting, where individuals with similar behavioral profiles aggregate at the same locations within the group. This can even result in groups splitting up into smaller, more homogeneous groups (Sumpter 2010). Although such effects of behavioral heterogeneity in groups have not yet been investigated in the context of collective vortex movements, it is reasonable to expect that they occur. For example, it is possible that individuals occupy different positions within vortices (e.g., outer edge, inner edge) depending on individual characteristics (e.g., speed) or physiological state (e.g., hunger). It is even possible that certain positions within vortices provide particular fitness benefits. For example, individuals closer to the core in a feeding tadpole vortex (see the section, Feeding Function and Access to Other Resources) may have access to more nutrients. Another interesting question would be to investigate whether heterogeneity of behavioral profiles within groups could increase the likelihood for vortices to be formed or maintained. For example, groups consisting of faster and slower individuals may be more likely to form vortices, as the faster individuals might begin to circle around the slower individuals. We suggest that more work is needed to improve our understanding of the role differences between individuals play in collective vortex movements.

Another aspect of critical importance to our understanding of collective vortex behaviors is the life span or the survival probability of this phenomenon in different species. With the exception of the work by Tunström et al. (2013), scientists only report the presence, but not the stability, of vortex movements. However, whether vortex movements are more or less stable and persistent than other group movement configurations (e.g., swarm, polarized school) could provide important insights into the mechanisms and ecological drivers underlying group movements. In order to achieve a better understanding of the stability of vortex movements, the mechanisms and likelihood for transitions between different movement states need to be investigated (as in Tunström et al. 2013). In addition, properties relating to the stability of vortex movements, such as the number of individuals leaving or joining the vortex and the probability of the vortex changing movement direction, could give important insights into the mechanisms underlying this movement phenomenon. For example, we do not know whether the frequency of changes in movement direction depends on the specific underlying proximate mechanisms or whether it is a universal property that only depends on the size or density of the animal aggregation involved. Comparative studies on such summary statistics between systems that generate vortex movements based on different proximate causes would be interesting in this regard.

Analysis of theoretical models, such as numerical simulations of individual-based models (e.g., Couzin et al. 2002; Gautrais et al. 2008) or analytic treatments of simplified mathematical models for group movement (e.g., Lukeman et al. 2009), has been crucial in illustrating potential mechanisms for vortex movements. Throughout the section, Mechanisms (Proximate Causes), we have given examples for how models have been used to verify the ability of proposed proximate mechanisms to produce vortex movements and to identify new, previously unknown proximate mechanisms. Furthermore, models have also been used to illustrate potential evolutionary pathways that could explain why animals display vortex movements (e.g., Kunz et al. 2006; Wood and Ackland 2007). In this way, models have been very successful in demonstrating the existence of vortex movements for different underlying mechanisms. It is beyond the scope of this review to establish in detail which current models for group movements do lead to the formation and maintenance of vortex behaviors. However, this highlights an area of future research for modelers: what are the conditions that are necessary to produce stable or unstable vortex movements, i.e., going beyond demonstrating the sufficient conditions of vortex formation? Such an investigation would help to develop a broader, less model-specific understanding of vortex movements in animals. As useful starting points for such an approach, simple, abstract models could be analyzed (e.g., Lukeman et al. 2009) or potential links to established theories on vortices in other fields, such as fluid dynamics (e.g., Batchelor 2000) or statistical physics (patterns of symmetry-breaking; e.g., José et al. 1977) could be explored.

We have seen that there are a number of potential ultimate causes for the adoption of vortex movements in different species. To date, hardly any of these potential ultimate causes have been tested in empirical or theoretical (e.g., simulation) experiments. Considering how ubiquitous and widespread across different species collective vortex movements are, we highly recommend further research into their ultimate causes. It is conceivable that the adoption of vortex movements across species could hint at common pathways for the evolution of collective movements.

Throughout, we have highlighted a problem with isolating ultimate causes for vortex movements: for some species, the same individual social behaviors can give rise to different collective behaviors depending on internal or external factors (e.g., circular trails in ants or the bistable state “vortex school” in fish). In this case, the question is whether vortex movements are (or can be) selected for because of the advantages they bring or whether vortex movements have an insufficient impact on individual fitness and are simply a byproduct of selection acting on social behaviors.

A last question that has not been investigated at all to date is the extent to which collective vortex movements could be behaviors that animal groups learn and adopt deliberately to derive certain benefits

from them (e.g., when feeding). Based on what is currently known, we suggest that collective vortex movements are typically not learned. The presence of vortex movements in *Spea multiplicata* and in the hybrid *S. multiplicata* × *bombifrons* tadpoles and their absence in *S. bombifrons* tadpoles even suggest a genetic origin to vortex behavior (Bazazi et al. 2012). We have seen that simple behavioral rules can produce collective vortex behaviors via interactions between individuals, and/or between individuals and their environment. Therefore, learned behaviors are not a necessary condition for vortices in animal groups.

CONCLUSIONS

First, a collective vortex movement is a set of individuals presenting a significant degree of aggregation and presenting a correlated radial motion around a common center. Our suggested definition is completely descriptive, without referring to the underlying process and function, nor to any taxa.

Second, collective vortex movements are ubiquitous and occur across a wide range of species. To date, they are not well understood, despite their ubiquity.

Third, a variety of proximate mechanisms can give rise to collective vortex behaviors, such as attraction to a local stimulus, indirect self-organization based on stigmergy, repulsion from surrounding environmental stimuli or constraints, direct self-organization by social interaction between individuals, instability induced by a gradient, and accidental positive feedback by pheromones. The minimal condition to obtain a vortex is an aggregation of individuals, the persistence of individual motion and a short-range social interaction (social repulsive force or, in extreme cases, simply a constraint effect such as collision and compaction).

Fourth, ultimate causes could vary across species and situations. Access to resources (nutrients, oxygen or light), antipredator function, locomotion, perhaps also improving collective decision-making and information transfers, are some of the potential benefits offered by performing vortex collective behaviors. At the moment, the state of knowledge about vortex function and evolution is very limited and fragmented and, with the exception of facilitating access to feeding resources, none of the suggested functions have empirical support.

Fifth, at present, very few studies explore the properties of collective vortex movements in biological systems in detail. New technologies, notably video multitracking techniques, now make these studies possible.

Finally, we suggest it is important to study collective vortex behaviors because understanding them could provide deep insights into the nature and evolution of social group movements.

ACKNOWLEDGMENTS

J. Delcourt and M. Denoël are respectively a Postdoctoral Researcher and a Senior Research Associate at the Fonds de la Recherche Scientifique (F.R.S.)—FNRS. N. W. F. Bode was supported by an AXA research fellowship and by the Leverhulme Trust. This is a publication of the Applied and Fundamental Fish Research Center (AFFISH-RC) of the University of Liège. This work was supported by the Fonds de la Recherche Scientifique—FNRS under F.R.F.C. Grants n° 2.4.617.08.F and 2.4.507.08.F. We are very grateful to A.-M. Massin and V. Briers for the drawings in Figure 1 and to C. Orban for her comments on the manuscript.

REFERENCES

- Alexander R. M. 2003. *Principles of Animal Locomotion*. Princeton (New Jersey): Princeton University Press.
- Aoki I. 1982. A simulation study on the schooling mechanism in fish. *Bulletin of the Japanese Society of Scientific Fisheries* 48:1081–1088.
- Batchelor G. K. 2000. *An Introduction to Fluid Dynamics*. Cambridge (United Kingdom): Cambridge University Press.
- Bazazi S., Buhl J., Hale J. J., Anstey M. L., Sword G. A., Simpson S. J., Couzin I. D. 2008. Collective motion and cannibalism in locust migratory bands. *Current Biology* 18:735–739.
- Bazazi S., Ioannou C. C., Simpson S. J., Sword G. A., Torney C. J., Lorch P. D., Couzin I. D. 2010. The social context of cannibalism in migratory bands of the Mormon cricket. *PLOS ONE* 5:e15118.
- Bazazi S., Pfennig K. S., Handegard N. O., Couzin I. D. 2012. Vortex formation and foraging in polyphenic spadefoot toad tadpoles. *Behavioral Ecology and Sociobiology* 66:879–889.
- Bearon R. N., Grünbaum D. 2006. Bioconvection in a stratified environment: experiments and theory. *Physics of Fluids* 18:127102.
- Beckers R., Holland O. E., Deneubourg J.-L. 1994. From local actions to global tasks: stigmergy and collective robotics. *Artificial Life* 4:181–189.
- Beebe W. 1921. *Edge of the Jungle*. New York: H. Holt and Company.
- Beecham J. A., Farnsworth K. D. 1999. Animal group forces resulting from predator avoidance and competition minimization. *Journal of Theoretical Biology* 198:533–548.
- Belmonte J. M., Thomas G. L., Brunnet L. G., de Almeida R. M. C., Chaté H. 2008. Self-propelled particle model for cell-sorting phenomena. *Physical Review Letters* 100:248702.
- Ben-Jacob E. 2003. Bacterial self-organization: co-enhancement of complexification and adaptability in a dynamic environment. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 361:1283–1312.
- Ben-Jacob E., Levine H. 2006. Self-engineering capabilities of bacteria. *Journal of the Royal Society Interface* 3:197–214.
- Ben-Jacob E., Cohen I., Czirók A., Vicsek T., Gutnick D. L. 1997. Chemomodulation of cellular movement, collective formation of vortices by swarming bacteria, and colonial development. *Physica A: Statistical Mechanics and its Applications* 238:181–197.
- Bode N. W. F., Delcourt J. 2013. Individual-to-resource landscape interaction strength can explain different collective feeding behaviours. *PLOS ONE* 8:e75879.
- Bode N. W. F., Faria J. J., Franks D. W., Krause J., Wood A. J. 2010. How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society B: Biological Sciences* 277:3065–3070.
- Bode N. W. F., Franks D. W., Wood A. J. 2011. Limited interactions in flocks: relating model simulations to empirical data. *Journal of the Royal Society Interface* 8:301–304.
- Buhl J., Sumpter D. J. T., Couzin I. D., Hale J. J., Despland E., Miller E. R., Simpson S. J. 2006. From disorder to order in marching locusts. *Science* 312:1402–1406.
- Bumann D., Krause J. 1993. Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). *Behaviour* 125:189–198.
- Bumann D., Krause J., Rubenstein D. 1997. Mortality risk of spatial positions in animal groups: the danger of being in the front. *Behaviour* 134:1063–1076.
- Burggren W. W., Bemis W. E. 1992. Metabolism and ram gill ventilation in juvenile paddlefish, *Polyodon spathula* (Chondrostei: Polyodontidae). *Physiological Zoology* 65:515–539.
- Calovi D. S., Lopez U., Ngo S., Sire C., Chaté H., Theraulaz G. 2014. Swarming, schooling, milling: phase diagram of a data-driven fish school model. *New Journal of Physics* 16:015026.
- Camazine S., Deneubourg J.-L., Franks N. R., Sneyd J., Theraulaz G., Bonabeau E. 2001. *Self-Organization in Biological Systems*. Princeton (New Jersey): Princeton University Press.

- Carlson J. K., Goldman K. J., Lowe C. G. 2004. Metabolism, energetic demand, and endothermy. Pages 203–224 in *Biology of Sharks and Their Relatives*, edited by J. C. Carrier, J. A. Musick, and M. R. Heithaus. Boca Raton (Florida): CRC Press.
- Carter A. J., Feeney W. E., Marshall H. H., Cowlshaw G., Heinsohn R. 2013. Animal personality: what are behavioural ecologists measuring? *Biological Reviews of the Cambridge Philosophical Society* 88:465–475.
- Charabidze D., Bourel B., Gosset D. 2011. Larval-mass effect: characterisation of heat emission by necrophagous blowflies (Diptera: Calliphoridae) larval aggregates. *Forensic Science International* 211:61–66.
- Choi Y., Jung E., Park H., Paik S. R., Jung S., Kim S. 2004. Construction of microbial fuel cells using thermophilic microorganisms, *Bacillus licheniformis* and *Bacillus thermoglucosidasius*. *Bulletin of the Korean Chemistry Society* 25:813–818.
- Cisneros L. H., Cortez R., Dombrowski C., Goldstein R. E., Kessler J. O. 2007. Fluid dynamics of self-propelled microorganisms, from individuals to concentrated populations. *Experiments in Fluids* 43:737–753.
- Couzin I. D. 1999. Collective Animal Behaviour. PhD diss., University of Bath.
- Couzin I. D. 2009. Collective cognition in animal groups. *Trends in Cognitive Sciences* 13:36–43.
- Couzin I. D., Franks N. R. 2003. Self-organized lane formation and optimized traffic flow in army ants. *Proceedings of the Royal Society B: Biological Sciences* 270:139–146.
- Couzin I. D., Krause J. 2003. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior* 32:1–75.
- Couzin I. D., Krause J., James R., Ruxton G. D., Franks N. R. 2002. Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology* 218:1–11.
- Czirók A., Vicsek T. 2000. Collective behavior of interacting self-propelled particles. *Physica A: Statistical Mechanics and its Applications* 281:17–29.
- Czirók A., Ben-Jacob E., Cohen I., Vicsek T. 1996. Formation of complex bacterial colonies via self-generated vortices. *Physical Review E* 54:1791–1801.
- Delcourt J., Poncin P. 2012. Shoals and schools: back to the heuristic definitions and quantitative references. *Reviews in Fish Biology and Fisheries* 22:595–619.
- Delcourt J., Yliff M. Y., Bolliet V., Poncin P., Bardonnet A. 2011. Video tracking in the extreme: a new possibility for tracking nocturnal underwater transparent animals with fluorescent elastomer tags. *Behavior Research Methods* 43:590–600.
- Delcourt J., Denoël M., Yliff M., Poncin P. 2013. Video multitracking of fish behaviour: a synthesis and future perspectives. *Fish and Fisheries* 14:186–204.
- Deneubourg J.-L., Goss S., Franks N., Pasteels J. M. 1989. The blind leading the blind: modeling chemically mediated army ant raid patterns. *Journal of Insect Behavior* 2:719–725.
- Deneubourg J.-L., Aron S., Goss S., Pasteels J. M. 1990. The self-organizing exploratory pattern of the argentine ant. *Journal of Insect Behavior* 3:159–168.
- Dombrowski C., Cisneros L., Chatkaew S., Goldstein R. E., Kessler J. O. 2004. Self-concentration and large-scale coherence in bacteria dynamics. *Physical Review Letters* 93:098103.
- Dorigo M., Bonabeau E., Theraulaz G. 2000. Ant algorithms and stigmergy. *Future Generation Computer Systems* 16:851–871.
- Dowd W. W., Brill R. W., Bushnell P. G., and Musick J. A. 2006. Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change. *Fisheries Bulletin* 104:323–331.
- Dyer J. R. G., Johansson A., Helbing D., Couzin I. D., Krause J. 2009. Leadership, consensus decision making and collective behaviour in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:781–789.
- Economakis A. E., Lobel P. S. 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes* 51:129–139.

- Fabre J.-H. 1899. *Souvenirs Entomologiques. Études sur l'Instinct et les Moeurs des Insectes*. Paris (France): Librairie Ch. Delagrave.
- Fitzgerald T. D. 2003. Role of a trail pheromone in the foraging and processionary behavior of pine processionary caterpillars *Thaumetopoea pityocampa*. *Journal of Chemical Ecology* 29:513–532.
- Foster K. W., Smydth R. D. 1980. Light antennas in phototactic algae. *Microbiological Reviews* 44:572–630.
- Franks N. R., Gomez N., Goss S., Deneubourg J.-L. 1991. The blind leading the blind in army ant raid patterns: testing a model of self-organization (Hymenoptera: Formicidae). *Journal of Insect Behavior* 4:583–607.
- Garnier S., Gautrais J., Theraulaz G. 2007. The biological principles of swarm intelligence. *Swarm Intelligence* 1:3–31.
- Gautrais J., Jost C., Theraulaz G. 2008. Key behavioural factors in a self-organised fish school model. *Annales Zoologici Fennici* 45:415–428.
- Gautrais J., Ginelli F., Fournier R., Blanco S., Soria M., Chaté H., Theraulaz G. 2012. Deciphering interactions in moving animal groups. *PLOS Computational Biology* 8:e1002678.
- Ghorai S., Hill N. A. 1999. Development and stability of gyrotactic plumes in bioconvection. *Journal of Fluid Mechanics* 400:1–31.
- Gooders J., Boyer T. 1986. *Ducks of North America and the Northern Hemisphere*. Reissue Edition. New York: Facts On File.
- Gotwald W. H. 1995. *Army Ants: The Biology of Social Predation*. Ithaca (New York): Comstock Publishing Associates, Cornell University Press.
- Grassé P.-P. 1959. La reconstruction du nid et les coordinations interindividuelles chez *Bellicositermes natalensis* et *Cubitermes* sp. La théorie de la stigmergie: essai d'interprétation du comportement des termites constructeurs. *Insectes Sociaux* 6:41–80.
- Grossman D., Aranson I. S., Ben-Jacob E. 2008. Emergence of agent swarm migration and vortex formation through inelastic collisions. *New Journal of Physics* 10:023036.
- Halloy J., Sempo G., Caprari G., Rivault C., Asadpour M., Tâche F., Saïd I., Durier V., Canonge S., Amé J. M., Detrain C., Correll N., Martinoli A., Mondada F., Siegwart R., Deneubourg J.-L. 2007. Social integration of robots into groups of cockroaches to control self-organized choices. *Science* 318:1155–1158.
- Hamilton W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Helbing D., Molnár P. 1995. Social force model for pedestrian dynamics. *Physical Review E* 51:4282–4286.
- Hemelrijk C. K., Reid D. A. P., Hildenbrandt H., Padding J. T. 2015. The increased efficiency of fish swimming in a school. *Fish and Fisheries* 16:511–521.
- Herbert-Read J. E., Krause S., Morrell L. J., Schaerf T. M., Krause J., Ward A. J. W. 2013. The role of individuality in collective group movement. *Proceedings of the Royal Society B: Biological Sciences* 280:20122564.
- Hill N. A., Pedley T. J. 2005. Bioconvection. *Fluid Dynamics Research* 37:1–20.
- Huth A., Wissel C. 1992. The simulation of the movement of fish schools. *Journal of Theoretical Biology* 156:365–385.
- James R., Bennett P. G., Krause J. 2004. Geometry for mutualistic and selfish herds: the limited domain of danger. *Journal of Theoretical Biology* 228:107–113.
- Johnsgard P. A. 1965. *Handbook of Waterfowl Behavior*. Ithaca (New York): Comstock Publishing Associates.
- José J. V., Kadanoff L. P., Kirkpatrick S., Nelson D. R. 1977. Renormalization, vortices, and symmetry-breaking perturbations in the two-dimensional planar model. *Physical Review B* 16:1217–1241.
- Kessler J. O. 1985a. Hydrodynamic focusing of motile algal cells. *Nature* 313:218–220.
- Kessler J. O. 1985b. Co-operative and concentrative phenomena of swimming micro-organisms. *Contemporary Physics* 26:147–166.

- Kils U. 1993. Formation of micropatches by zooplankton-driven microturbulences. *Bulletin of Marine Science* 53:160–169.
- Kitsunezaki S., Komori R., Harumoto T. 2007. Bioconvection and front formation of *Paracemium tetraurelia*. *Physical Review E* 76:046301.
- Krause J., Bumann D., Todt D. 1992. Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). *Behavioral Ecology and Sociobiology* 30:177–180.
- Krause J., Reeves P., Hoare D. 1998. Positioning behaviour in roach shoals: the role of body length and nutritional state. *Behaviour* 135:1031–1039.
- Krause J., Hoare D., Krause S., Hemelrijk C. K., Rubenstein D. I. 2000. Leadership in fish shoals. *Fish and Fisheries* 1:82–89.
- Kunz H., Züblin T., Hemelrijk C. K. 2006. On prey grouping and predator confusion in artificial fish schools. Pages 365–371 in *Artificial Life X: Proceedings of Tenth International Conference on the Simulation and Synthesis of Living Systems*, edited by L. M. Rocha, L. S. Yaeger, M. A. Bedau, D. Floreano, R. L. Goldstone, and A. Vespignani. Cambridge (Massachusetts): MIT Press.
- Kuznetsov A. V. 2005. Thermo-bioconvection in a suspension of oxytactic bacteria. *International Communications in Heat and Mass Transfer* 32:991–999.
- Lima S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour* 49:11–20.
- Lukeman R., Li Y.-X., Edelstein-Keshet L. 2009. A conceptual model for milling formations in biological aggregates. *Bulletin of Mathematical Biology* 71:352–382.
- Mach R., Schweitzer F. 2007. Modeling vortex swarming in *Daphnia*. *Bulletin of Mathematical Biology* 69:539–562.
- Mann R. P., Perna A., Strömbom D., Garnett R., Herbert-Read J. E., Sumpter D. J. T., Ward A. J. W. 2012. Multi-scale inference of interaction rules in animal groups using Bayesian model selection. *PLOS Computational Biology* 8:e1002308.
- Marras S., Killen S. S., Lindström J., McKenzie D. J., Steffensen J. F., Domenici P. 2015. Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology* 69:219–226.
- Michelena P., Jeanson R., Deneubourg J.-L., Sibbald A. M. 2010. Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B: Biological Sciences* 277:1093–1099.
- Milgram S., Toch H. 1969. Collective behaviour: crowds and social movements. Pages 507–610 in *The Handbook of Social Psychology*, Second Edition, edited by G. Lindzey and E. Aronson. Reading (Massachusetts): Addison-Wesley Publishing Company.
- Miller N., Garnier S., Hartnett A. T., Couzin I. D. 2013. Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences of the United States of America* 110:5263–5268.
- Mitri S., Wischmann S., Floreano D., Keller L. 2013. Using robots to understand social behaviour. *Biological Reviews* 88:31–39.
- Mogami Y., Yamane A., Gino A., Baba S. A. 2004. Bioconvective pattern formation of *Tetrahymena* under altered gravity. *Journal of Experimental Biology* 207:3349–3359.
- Morton T. L., Haefner J. W., Nugula V., Decino R. D., Mendes L. 1994. The selfish herd revisited: do simple movement rules reduce relative predation risk? *Journal of Theoretical Biology* 167:73–79.
- Moussaïd M., Helbing D., Garnier S., Johanson A., Combe M., Theraulaz G. 2009. Experimental study of the behavioural mechanisms underlying self-organization in human crowds. *Proceedings of the Royal Society B: Biological Sciences* 276:2755–2762.
- Moussaïd M., Helbing D., Theraulaz G. 2011. How simple rules determine pedestrian behavior and crowd disasters. *Proceedings of the National Academy of Sciences of the United States of America* 108:6884–6888.

- Nill D., Siemers B. 2001. *Fledermäuse—eine Bildreise in die Nacht*. München (Germany): BLV Verlagsgesellschaft mbH.
- Ochiai N., Dragiila M. I., Parker J. L. 2011. Pattern swimming of *Phytophthora citricola* zoospores: an example of microbial bioconvection. *Fungal Biology* 115:228–235.
- O’Neal Campbell M. 2015. *Vultures: Their Evolution, Ecology and Evolution*. Boca Raton (Florida): CRC Press, Taylor & Francis.
- Ordemann A., Balazsi G., Moss F. 2003. Pattern formation and stochastic motions of the zooplankton *Daphnia* in a light field. *Physica A: Statistical Mechanics and its Applications* 325:260–266.
- Parr A. E. 1927. A contribution to the theoretical analysis of the schooling behavior of fishes. *Occasional Papers of the Bingham Oceanographic Collection* 1:1–32.
- Parrish J. K., Viscido S. V., Grünbaum D. 2002. Self-organized fish schools: an examination of emergent properties. *Biological Bulletin* 202:296–305.
- Pennycuik C. J. 2008. *Modelling the Flying Bird*. Burlington (Massachusetts): Academic Press.
- Perna A., Granovskiy B., Garnier S., Nicolis S. C., Labédan M., Theraulaz G., Fourcassie V., Sumpter D. J. T. 2012. Individual rules for trail pattern formation in Argentine ants (*Linepithema humile*). *PLOS Computational Biology* 8:e1002592.
- Platt J. R. 1961. “Bioconvection patterns” in cultures of free-swimming organisms. *Science* 133:1766–1767.
- Rappel W.-J., Nicol A., Sarkissian A., Levine H., Loomis W. F. 1999. Self-organized vortex state in two-dimensional *Dictyostelium* dynamics. *Physical Review Letters* 83:1247–1250.
- Reynolds C. W. 1987. Flocks, herds, and schools: a distributed behavioural model. *Computer Graphics* 21:25–34.
- Rieucan G., Martin J. G. A. 2008. Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. *Oikos* 117:501–506.
- Robertson B. A., Rehage J. S., Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution* 28:552–560.
- Schneirla T. C. 1944. A unique case of circular milling in ants, considered in relation to trail following and the general problem of orientation. *American Museum Novitates* 1253:1–26.
- Schneirla T. C. 1971. *Army Ants: A Study in Social Organization*. San Francisco (California): W. H. Freeman.
- Shitanda I., Yoshida Y., Tatsuma T. 2007. Microimaging of algal bioconvection by scanning electrochemical microscopy. *Analytical Chemistry* 79:4237–4240.
- Sih A., Bell A. M., Johnson J. C., Ziemba R. E. 2004. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79:241–277.
- Silverberg J. L., Bierbaum M., Sethna J. P., Cohen I. 2013. Collective motion of humans in mosh and circle pits at heavy metal concerts. *Physical Review Letters* 110:228701.
- Stuart D. 1994. *Bats: Mysterious Flyers of the Night*. Minneapolis (Minnesota): Carolrhoda Books.
- Sumpter D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 361:5–22.
- Sumpter D. J. T. 2010. *Collective Animal Behavior*. Princeton (New Jersey): Princeton University Press.
- Theraulaz G., Bonabeau E. 1999. A brief history of stigmergy. *Artificial Life* 5:97–116.
- Todd F. S. 1979. *Waterfowl: Ducks, Geese and Swans of the World*. New York: Sea World Press.
- Tunstrøm K., Katz Y., Ioannou C. C., Huepe C., Lutz M. J., Couzin I. D. 2013. Collective states, multistability and transitional behavior in schooling fish. *PLOS Computational Biology* 9:e1002915.
- Viscido S. V., Parrish J. K., Grünbaum D. 2004. Individual behavior and emergent properties of fish schools: a comparison of observation and theory. *Marine Ecology Progress Series* 273:239–249.
- Vollmer J., Vegh A. G., Lange C., Eckhardt B. 2006. Vortex formation by active agents as a model for *Daphnia* swarming. *Physical Review E* 73:061924.
- Wager H. 1911. On the effect of gravity upon the movements and aggregation of *Euglena viridis*, Ehrb. and other micro-organisms. *Philosophical Transaction of the Royal Society of London B: Biological Sciences* 201:333–390.

- Wegner N. C., Sepulveda C. A., Bull K. B., Graham J. B. 2010. Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: scombrids and billfishes. *Journal of Morphology* 271:36–49.
- Wheeler W. M. 1910. *Ants, their Structure, Development and Behavior*. New York: Columbia University Press.
- Williams C. R., Bees M. A. 2011. A tale of the three taxes: photo-gyro-gravitactic bioconvection. *Journal of Experimental Biology* 214:2398–2408.
- Wood A. J., Ackland G. J. 2007. Evolving the selfish herd: emergence of distinct aggregating strategies in an individual-based model. *Proceedings of the Royal Society B: Biological Sciences* 274:1637–1642.